ON THE OCCURRENCE AND SIGNIFICANCE OF "BARS" OR "RIMS" OF SANIO IN THE CYCADS

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(WITH PLATE XV)

The "bars" or "rims" of Sanio were probably first figured by GÖPPERT (2) in 1849, as has been pointed out by Miss GERRY (1). SANIO (7), however, did not, as she states, claim to be the discoverer of them, although he was the first to describe them at all adequately, and hence they have borne his name. In studying the development of the wood cells in *Pinus silvestris*, he found thickened rings, complete or incomplete, which grew up around thin spots in the cellulose primary walls. The thin areas he designated as the "Primordialtüpfeln," and on these bordered pits were formed. The thickened rims, or "Umrissen," of these areas are the structures that have until recently been known as the "bars of Sanio." In 1913 GROOM and RUSHTON (3) applied the name "rims" to them. This term is descriptive of SANIO's theory of their method of formation and serves to distinguish them from trabeculae.

Until the last few years they did not come into much prominence, but in several recent papers they have been considered of great importance. Miss GERRY, in the paper mentioned above, gave a comprehensive account of their distribution in the conifers. She found them in all the members of this group except the araucarians, whose wood structure could in this way be distinguished from the other forms. She also suggests the extension of this distinction to the fossil forms, as the following sentence indicates: "The distribution of the bars of Sanio . . . . establishes a constant and useful diagnostic character in the determination of fossil woods" (p. 122). She would associate all the fossil conifers which have the "rims" with the Abietineae, and those which do not exhibit them with the Araucarineae, regardless of other characteristics of their tracheary structure.

Miss GERRY'S suggestion has been followed in a number of recent articles on fossil plants. Miss HOLDEN (**4, 5**) has used it in several papers. Her statement of the importance of the "rims" is even stronger than that of Miss GERRY, making their occurrence "by far the most reliable criterion for diagnosing coniferous woods" (**5,** p. 252). Again, in another paper she speaks still more strongly: "Comparative examination of living and fossil forms leads to the rejection of all criteria except cellulose bars of Sanio as an infallible test for tribal affinities" (**4,** p. 544).

JEFFREY (**6**) has also attached much weight to it, especially since his discovery in 1912 of what he considers a vestigial bar in the araucarian cone axis. His conclusion from its presence here is stated as follows: "*Agathis* and *Araucaria* have obviously come from ancestors which, in accordance with the accepted principles of comparative anatomy, had . . . . bars of Sanio in their tracheids" (p. 548). The phylogenetic significance which he attached to its occurrence in this position figures prominently in his theory of the abietinean ancestry of the Araucarineae. Recognizing that his conclusion from its occurrence in the araucarian cone axis would be invalidated if the same condition were found to occur in similar regions of forms such as the cycads, JEFFREY examined the primitive regions of *Cycas*, *Zamia*, and *Ginkgo*, but found no evidence of its presence. He was therefore doubly assured of its meaning in the araucarians.

In connection with some investigations of the wood structure in the cycads, I have found a "bar"[1] of Sanio entirely similar to that in the araucarians, and since this discovery has such an important bearing on the theories above stated, it has been thought advisable to publish it separately.

The material in which the "bars" were found is from the petiole of *Cycas revoluta*. The sections of this, as well as all the others figured in the plate, were stained in the usual way with a double stain of Haidenhain's iron-hematoxylin and safranin. The bars thus appear in the sections as dark bands on a red background and stand out as distinctly as in the photographs.

[1] The name "bar" has been retained in this paper for the structure as found in *Araucaria* and *Cycas*, for considerations to be stated later.

Fig. 1 is from a section of the vascular bundle of the *Cycas* petiole cut so as to show the tangential walls of the tracheids of the primary wood. Spiral and scalariform elements of the xylem are shown at the left center of the figure, while the two transitional tracheids to the right of these exhibit the border-pitted condition typical of the region. Crossed pores can be seen in several of the pits, showing that the walls are not adjacent to parenchyma, but separate the lumina of two tracheids. The dark lines observable between the pits are thickenings in the primary wall and constitute the "bars of Sanio."

Fig. 3 is a portion of fig. 1 at a higher magnification and shows the part of the two border-pitted tracheids represented between (*a*) and (*b*) on that figure. The knife has passed diagonally through the wall of the left tracheid, leaving only a portion of one of the secondary layers, with parts of the primary attached to it in the upper region. In this area the bars of Sanio come out clearly, especially in connection with the fourth to the seventh pits from the top of the series.

The forking which has been mentioned by JEFFREY as occurring in the bars which he found in the araucarian cone axis is indicated here. An extreme instance of this can be seen between the fifth and sixth pits from the top. These pits are farther apart than is usual, and the bar instead of having merely its ends forked is cleft throughout its length, half clinging to each pit, as a definite "rim" of Sanio. This seems to indicate a double origin for the bars, suggesting that each may have its origin in two "rims," formed in the manner indicated by SANIO, one in connection with each pit. In the tracheid at the right, the bars are very plainly visible, though the forking is not so evident.

The "rims" which form the bars in *Cycas* are characterized especially by two features. They invariably cling closely to the borders of the pits, and they are short, never reaching across the entire width of a tracheid, but only across that of a single pit. These are the two characteristics mentioned by THOMSON (8) as distinguishing the type of bar found in the Araucarineae from that in the members of the Abietineae.

Fig. 4 is from the cone axis of *Araucaria Bidwilli* and shows the structures referred to by JEFFREY as occurring there. Here again, in the upper part of the figure, the wall has been partly cut away. The photograph is at the same magnification as fig. 3, and on comparison it will be seen that the characters of the bars in the two are identical. Here also they invariably cling closely to the pit borders and extend only across the width of a single pit. In almost every case the forking is plainly seen. A very favorable place for observing this is in the left hand tracheid at about the center of the figure. Near the top of this tracheid and in the majority of cases in the other two, the pits are so closely approximated horizontally, owing to the multiseriate character of the pitting, that the ends of the forks of adjacent bars meet, so that only more or less trapeziform lighter areas are seen between them. At one place, indeed, below the center of the middle tracheid, even this is not shown. It is quite evident, however, that this is not a case of a single bar passing across two pits, but of the application of two bars to each other, end to end. This is more evident from the section than from the photograph, for in it a light area similar to those shown in the series above, though not so pronounced, is visible.

There are, therefore, bars in the primitive region of *Cycas* exactly comparable to those in the araucarian cone axis. This, as JEFFREY recognized, makes their presence in the araucarian cone axis valueless as an argument in favor of abietinean ancestry of the Araucarineae. Indeed, the evidence of a reverse relationship is apparent from a study of the characters of the "bar" in the different regions of the Abietineae themselves.

The typical condition in old stem wood of the Abietineae is illustrated in fig. 2, a radial section of *Abies amabilis*. Where the pits are closely approximated in vertical series, as for example in the left tracheid of the figure or in the lower part of the tracheid to the right, the "rims" unite to form bars. Where the pits are scattered, as in the central part of the middle tracheid, each "rim" stands by itself. In neither case, however, are the "rims" closely appressed to the pit borders, as is always true in the araucarian and cycad form. They are not, moreover, limited in length

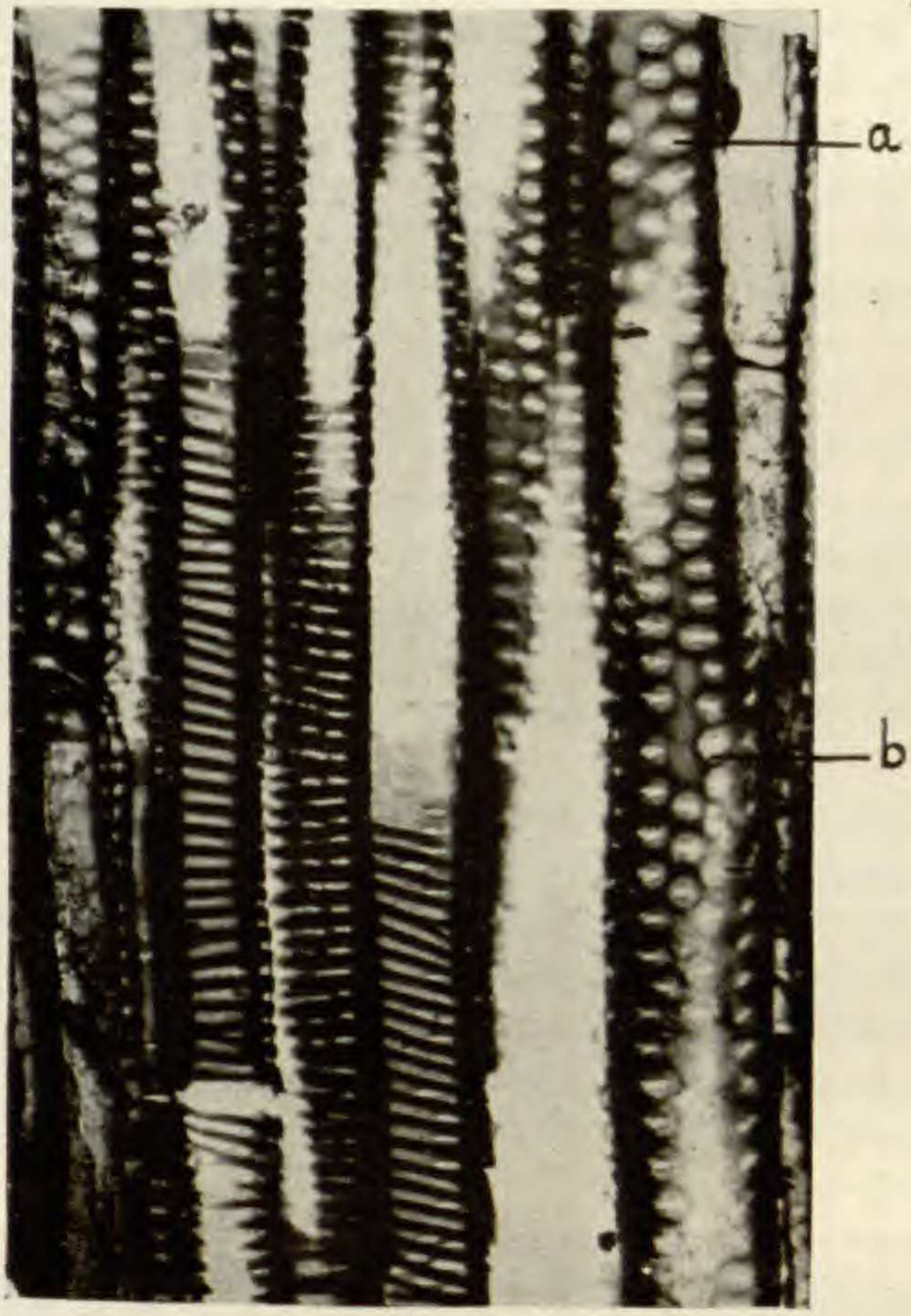
to the width of a single pit. This is especially striking in the tracheid to the left, where opposition and even multiseriate pitting is in evidence.

In fig. 5 is shown a section of the wood of the cone axis of *Pinus resinosa* near the primary xylem. It was difficult to get a good photograph on account of the irregularities in the tracheid walls. The figure illustrates the type of "rim" found in this region. The structures usually adhere closely to the pit borders, appearing as dark arcs, and not extending beyond the pits. One long bar, however, is shown just below the four pits at the top of the tracheid, passing across nearly the width of two pits, and thus presenting to some extent the appearance of the bar found in specialized abietinean wood. Such structures are exceptional.

Fig. 6, from a radial section of the root of *Pinus Strobus*, shows a condition quite often found in the secondary wood close to the primary. Although the pits are large, the "rims" of Sanio, which are plainly in evidence, present the same characters as those of fig. 5. As one passes out from this region into the outer root wood, transitions are seen between this rim and the type shown in fig. 2. The rims become more and more separated from the pits. They also elongate and exhibit a tendency to fusion. The mature bar is thus often a complex structure and very specialized in character. Similar transitions are seen in the cone axis in passing outward from the center.

It is generally admitted that root and cone axis retain ancestral characters longer than the stem or branches, and the earliest formed parts of these are also accounted more primitive than the parts formed when the plant is older. If in this case the accepted reasoning holds true, the Abietineae must have been derived from ancestors which had bars of the araucarian or cycadean type.

The discovery of "bars" or "rims" of Sanio in the primitive region of the cycads must either nullify their value as evidence of the derivation of the araucarians from the Abietineae, or indicate that the Abietineae are also ancestral to the cycads, a position which can scarcely be assumed. Moreover, the study of the rims in different regions of the Abietineae indicates that the ancestral type of bar, as found in the cycads and araucarians, has become



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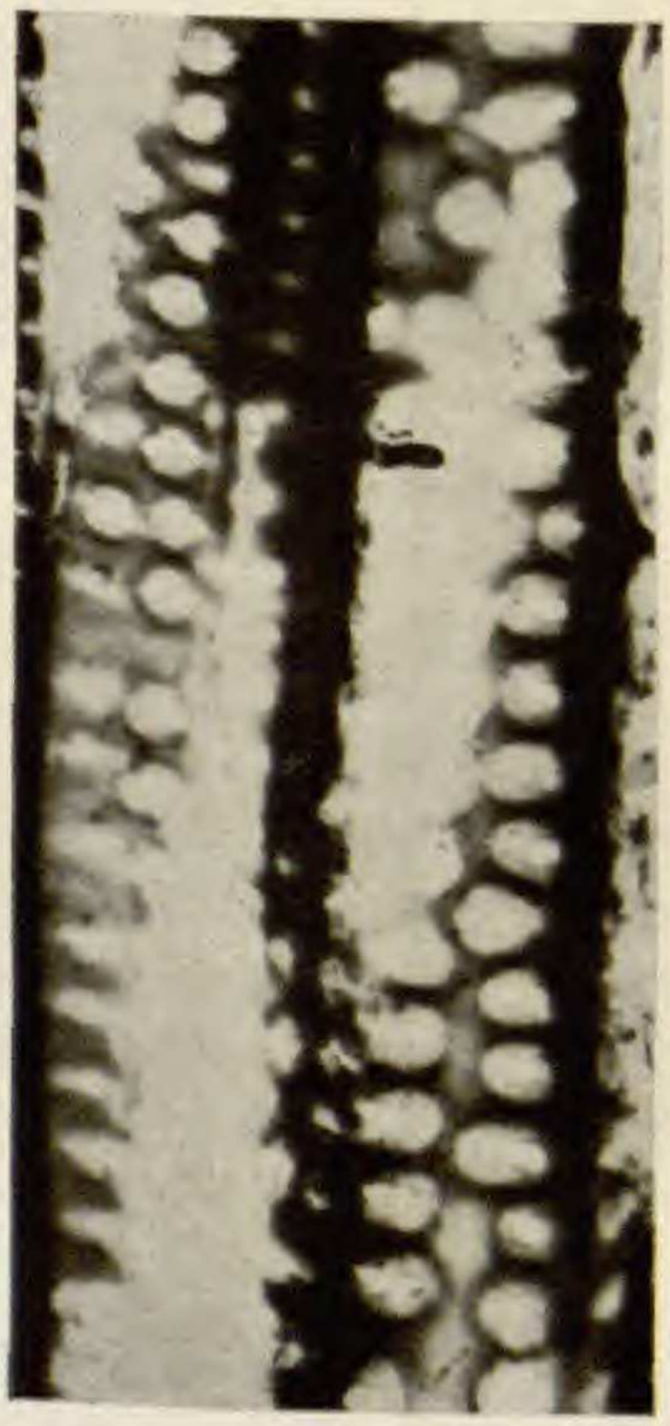

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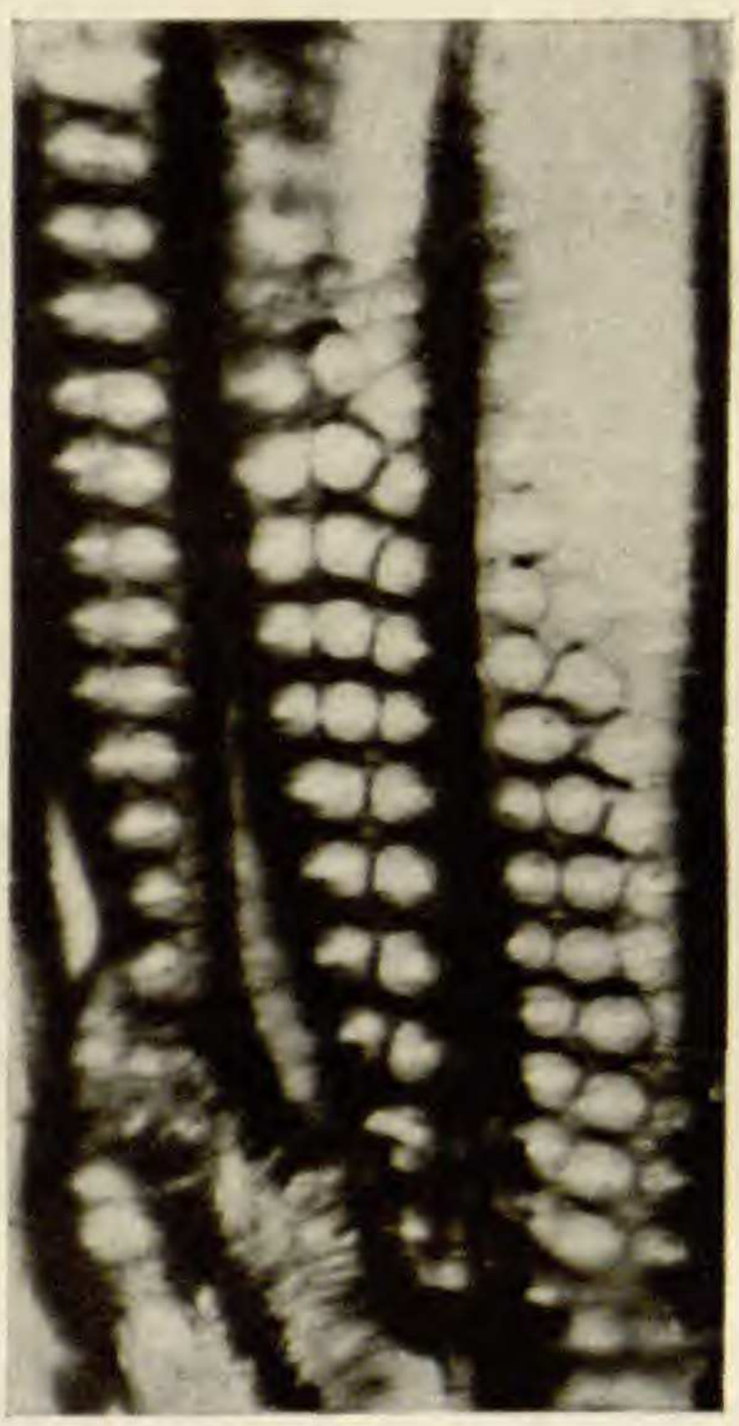

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SIFTON on BARS OF SANIO